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The Impact of Prolonged, Above-Normal Flooding on Metaphyton in a Freshwater Marsh*

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Abstract: The mean biomass of metaphyton was estimated at monthly intervals during the summer of 1982 in cells that had been flooded to 1 m above normal for 1 and 2 years and in control cells in an experimental marsh complex, located in the Delta Marsh, Manitoba, Canada. In 1982, cells flooded in 1981 had their highest mean algal biomass in June and July. It gradually declined through September, with an annual mean of 66 g m^{-2}. In cells flooded in 1982 and in control cells, mean algal biomass was significantly lower than in 2-year flooded cells; their mean biomass over the growing season were 20 g m^{-2} and 2.6 g m^{-2}, respectively. In the 1-year flooded treatment, mean algal biomass was highest in September; in the control, it peaked in June. Mean algal biomass during the growing season and among treatments was not correlated with any chemical parameter measured but did vary significantly among different kinds of habitats within the cells, being highest in areas dominated by standing emergent litter.

INTRODUCTION

Metaphyton, though an important component of freshwater marshes, generally have been overlooked by researchers. It is sometimes difficult to delineate this community from loosely associated epiphyton, but normally they are not sampled when periphyton or phytoplankton are sampled. Neverthe-

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less, metaphyton may attain high densities and have a high annual primary production (Weller and Fredrickson, 1974; Komarkova and Marvan, 1978). Representatives from many genera of freshwater algae, including species of *Oedogonium, Cladophora, Rhizoclonium, Microspora, Ulothrix, Tribonema, Enteromorpha, Vaucheria,* and *Hydrodictyon,* can be found as floating masses in aquatic systems (Hillebrand, 1983). In the Netherlands, floating masses of filamentous algae are collected from ponds and lakes and used as fertilizer; the Dutch language even has a common name for this group of algae, *flab* (Hillebrand, 1983). In freshwater marshes, metaphyton, however, differ from the free-floating *flab* because they are entangled with standing litter and emergent vegetation.

Little is known about the impact of water level fluctuations on metaphyton, although water level fluctuations are a characteristic feature of many wetlands, particularly prairie wetlands (van der Valk and Davis, 1978). Harris and Marshall (1963) have reported that green algae sometimes formed thick mats in recently reflooded wetlands. Likewise, Weller and Fredrickson (1974) found a significant increase in algal mats in Rush Lake, Iowa, after reflooding.

The objectives of this study were to investigate the impact of 1 and 2 years of abnormally high water levels on the biomass of metaphyton in a prairie marsh.

MATERIALS AND METHODS

Study Site

This study was conducted in the experimental marsh complex of the Marsh Ecology Research Program (MERP) at the Delta Waterfowl and Wetlands Research Station, Delta, Manitoba (50°11′N, 98°19′W). Ten experimental marshes (approximately 5 ha each) were constructed by diking an area within the Delta Marsh (Batt et al., 1983; Murkin et al., 1985; Murkin and Kadlec, 1986). Two comparable areas at each end of the experimental complex served as control cells.

The Delta Marsh is composed of large expanses of emergent vegetation, primarily dominated by *Phragmites australis, Scolochloa festucacea, Typha glauca,* and *Scirpus lacustris,* plus many areas free of emergents, called bays, which vary in size from a few to several hundred hectares (Love and Love, 1954). The water in the lake and marsh is slightly brackish with conductivities ranging from 1.8 to 3.3 mmhos (Bossenmaier, 1968). The initial vegetation within the experimental cells was similar to that in the main Delta Marsh (Pederson, 1983). There were four monodominant bands or zones of emergent species in all the cells of the experimental complex in 1980, with *Scolochloa festucacea* and *Phragmites australis* at the higher elevations, followed by *Typha glauca* and *Scirpus lacustris* at the lowest elevations.

The cells of the experimental complex were constructed during the winter of 1979–1980; during 1980, their water control structures were left open. Experimental water level manipulations began in 1981 when eight cells were flooded to 1 m above normal. The two remaining cells were flooded to 1 m above normal in 1982 (Batt et al., 1983; Murkin et al., 1985). Water levels in the two control cells were not manipulated in any way. In 1982, when this study was conducted, there were two control cells, two cells flooded that

spring, which we will refer to as the 1-year flooded treatment, and eight cells flooded the previous year, which we will refer to as the 2-year flooded treatment. The unequal replication of flooding treatments is a result of the overall experimental design of MERP (Batt et al., 1983; Murkin et al., 1985).

Most emergent vegetation was killed during the first year of flooding and, as a consequence, flooded marshes had a high density of standing litter, particularly dead *Phragmites* and *Typha* shoots. In the 2-year flooded treatment, portions of dead shoots below the waterline remained standing.

Field Sampling

Each of the 12 marshes was divided from north to south into 10 zones, and four of these were randomly selected in each marsh. Within each zone, four sampling sites were selected randomly for a total of 16 sites per marsh. Each cell was sampled four times (June, July, August, and September) for a total of 64 samples per cell over the growing season.

Eight habitat types were identified in the MERP complex: open water (no emergent or submersed vegetation), beds of submersed vegetation, stands of living *P. australis* and *S. lacustris*, and areas dominated by *Phragmites*, *Scirpus*, and *Typha* litter. The random samples collected in the cells were assigned to one of these habitat types to examine the impact of habitat on metaphyton biomass.

From a boat, metaphyton were sampled with a pole that had a series of stiff hooked wires protruding from one end, collectively delimiting a surface area of about 200 cm^2 (Fig. 1). The pole was pushed down to the bottom at a

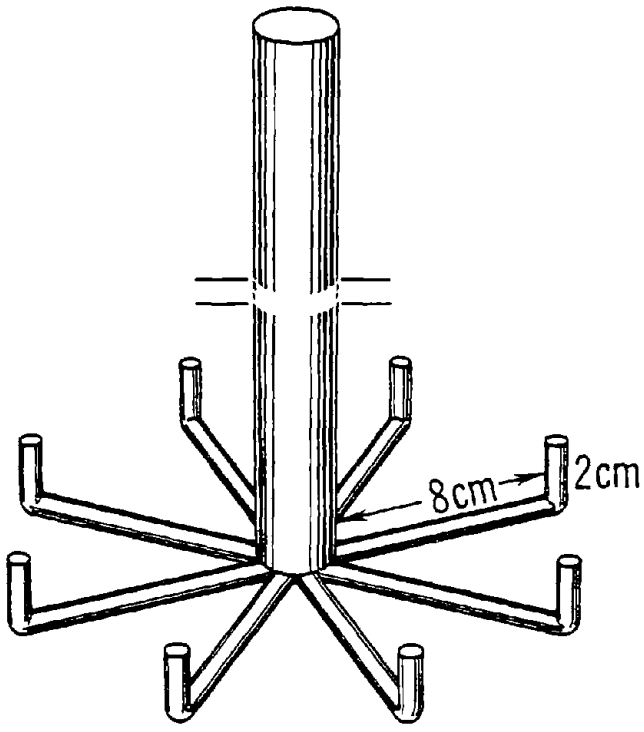

Fig. 1 Metaphyton sampler.

sampling site and then slowly raised. In the field, all metaphyton were removed from the prongs and transferred to a plastic bag. In the laboratory, macroinvertebrates, submersed plants, litter, and other debris were removed by hand from each sample. Cleaned samples were placed in preweighed aluminum pans, dried at 105°C for 24 hours, weighed, ashed at 500°C for a minimum of 3 hours, and then reweighed to obtain their ash-free dry weight (Vollenweider, 1974).

Water depth, temperature, pH, alkalinity, and specific conductance were measured whenever a sample was collected. Over the growing season, ammonia, nitrate, total dissolved nitrogen (TDN), soluble reactive phosphorus, and total dissolved phosphorus (TDP) were measured (Kadlec, 1986a, 1986b) using standard techniques. All analyses were done by the Freshwater Institute, Department of Fisheries and Oceans, Winnipeg, Canada (Stainton et al., 1977), and these data were used to examine correlations between metaphyton biomass and water chemistry.

Statistical Tests

Biomass estimates were analyzed using an ANOVA (using the GLM procedure in the Statistical Analysis System; SAS Institute Inc., 1982); the classification variables were cell, treatment, and their interactions. SAS also was used to compare treatment means (LSDs) and to calculate Pearson correlation coefficients between different environmental parameters and metaphyton biomass. All tests of significance were done at the 0.05 level.

RESULTS

The mean biomass over the growing season (66.3 g m^{-2}) of metaphyton in cells flooded for 2 years was significantly higher than in both 1-year flooded (20.1 g m^{-2}) and control (2.6 g m^{-2}) cells. The metaphyton biomass of cells flooded 1 year was not significantly different from that in the controls.

The mean biomass over the growing season in the 2-year flooded treatment ranged from 19.6 to 150.7 g m^{-2} (Table 1). Four of the marshes flooded for 2 years had extensive areas covered with dead *Phragmites* and *Typha* shoots. These marshes had a mean biomass of 101 g m^{-2}, three times higher than that of the other four marshes (31.5 g m^{-2}).

Mean monthly biomass was highest in the controls in June, in 1-year flooded cells in September, and in 2-year flooded cells in July (Fig. 2). Over the growing season, biomass seems to increase in the 1-year treatment but decrease in the 2-year treatment.

Metaphyton biomass in flooded cells was highest in habitats dominated by emergent litter (Fig. 3), while in control cells open water areas had the highest biomass. In all habitats in cells flooded for 2 years, there was more biomass than in similar habitats in 1-year flooded and control cells.

No significant correlation was found between any physicochemical parameter and metaphyton biomass, either over the growing season or among treatments.

DISCUSSION

The death of emergent macrophytes in flooded cells seems to have created habitats that stimulated metaphyton growth. Within a flooded cell, sites

TABLE 1

Annual Mean of Ash-Free Dry Biomass (g m^{-2}) of Metaphyton in Control Cells and Cells Flooded for 1 Year and 2 Years in 1982 (n = 64)

Marsh	Mean	±SE
	Control	
11	0.4	0.2
12	4.8	2.0
	1-Year flooded	
3	26.7	6.7
7	13.4	9.9
	2-Year flooded	
1	29.4	5.1
2	50.3	4.5
4	150.7	24.5
5	38.9	6.4
6	91.2	31.1
8	38.2	9.9
9	112.0	35.1
10	19.6	8.3

with dead standing emergent litter had a higher biomass than other habitats.

In control cells, open water sites had higher mean biomass than shaded sites with emergent macrophytes, probably due to the shading by the emer-

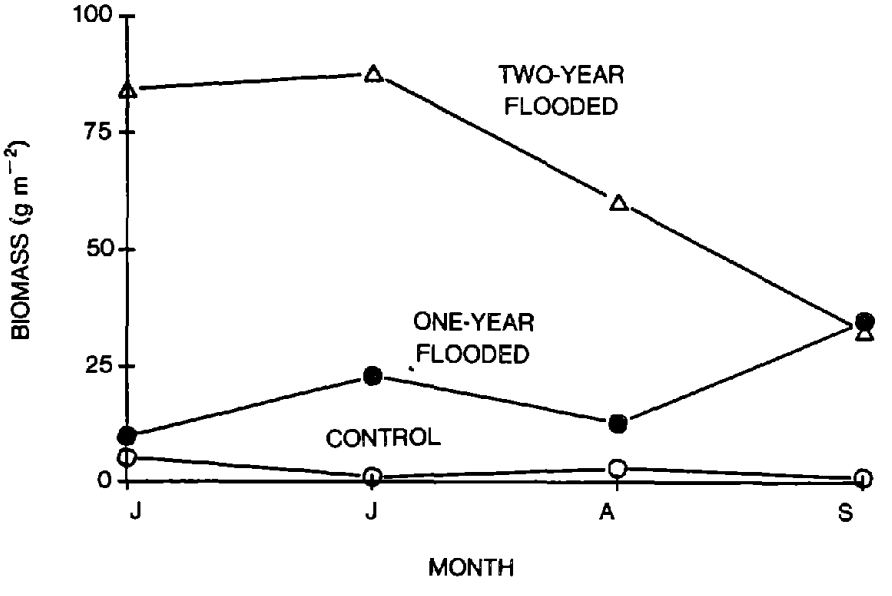

Fig. 2 Mean ash-free dry biomass (g m^{-2}) of metaphyton over the growing season in control cells and cells flooded for 1 year or 2 years in 1982.

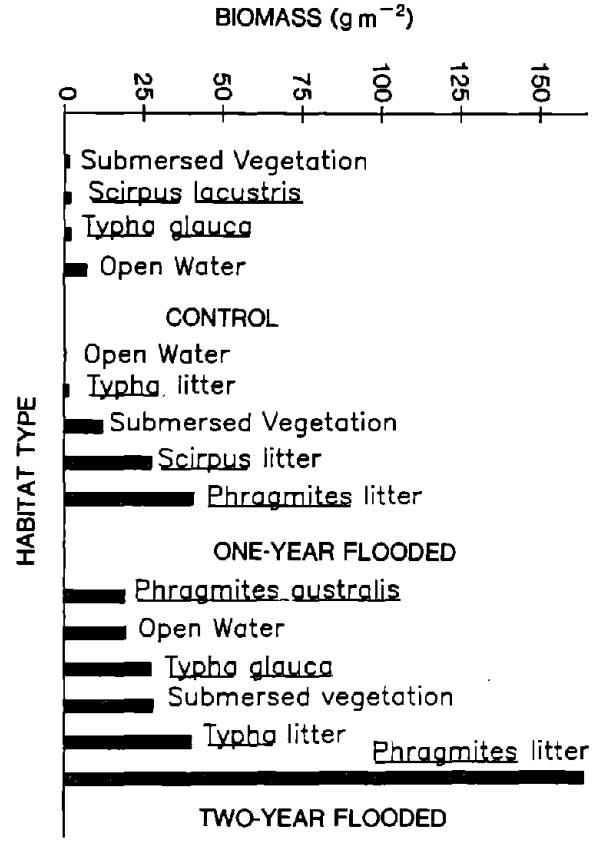

Fig. 3 Mean biomass of metaphyton (g m^{-2}) in different habitat types in the control, 1-year flooded, and 2-year flooded cells of the MERP complex during the 1982 growing season. Note: Not all habitats types are found in a treatment.

gent canopy. In 1-year flooded cells, the gradual death of emergent macrophytes over the 1982 growing season is accompanied by an increase in their metaphyton biomass (Fig. 2). This seasonal pattern was not found in the other two treatments. Collectively, these results suggest that an increase in light contributed to the increase in metaphyton biomass that occurred when cells are flooded. This is consistent with other studies on the impact of emergent canopies on algal photosynthesis, e.g., Straskraba and Pieczynska (1970). Hillebrand (1983) also indicated that *flab* abundance is light-dependent, and vertical ascent of metaphyton is only possible when a sufficient amount of light reaches the bottom. The primary production of epiphytic algae (Hooper and Robinson, 1976; Hosseini and van der Valk, 1988) is also stimulated by the death of the emergent canopy.

Light intensity, however, cannot be the only factor regulating metaphyton production because open water areas in the control cells did not have high metaphyton biomass (Fig. 3). Other factors such as differences in temperature, substrate (litter) abundance, water depth, and nutrient levels between flooded and control cells also must play a role. Unfortunately, very little is known about these differences in physicochemical conditions between flooded and nonflooded cells.

One *a priori* reason to expect higher metaphyton biomass in flooded cells is higher nutrient concentrations in the water column due to the release of nutrients by dying or dead macrophytes. This seems not to be a factor, since mean TDN and TDP concentrations were similar in both flooded treatments in 1982 and lower than in control cells (Kadlec, 1986a); there is no correlation between any physicochemical parameters measured and metaphyton biomass. However, the lack of any correlation does not eliminate the possibility that more nutrients were available in the flooded cells. Nutrients released by dying plants and fresh litter might be quickly taken up and not be detected by sampling at the time intervals used in this study. One striking difference between the control cells and the flooded cells is phytoplankton production. It is an order of magnitude higher in the control cells (Hosseini and van der Valk, 1988). Why metaphyton production and not phytoplankton production should be stimulated by flooding is not at all clear.

In a study of the impact of metaphyton litter on recruitment of species in these same cells in 1983 and 1984, when they were free of standing water, van der Valk (1986) found that areas with thick algal mats in the spring of 1983 had a mean biomass of about 200 g m^{-2}. This is the same order of magnitude as that found in the most productive habitats of cells in the 2-year treatment, and these are the areas that van der Valk was sampling (Table 1).

The sampler used in this study enabled us to quickly and efficiently sample metaphyton biomass in the three flooding treatments so that we could compare treatment effects. We wanted a sampler that would provide us a reliable index of metaphyton biomass. It is likely that this sampler underestimates metaphyton biomass in areas of low biomass and overestimates it in areas of high biomass. If this sampler is to be used to estimate the absolute biomass, a careful evaluation of its efficiency in sampling mats of different densities and thicknesses should be made.

The study of the role and significance of metaphyton in wetlands is obviously just beginning. This study illustrates that the biomass of these algae increases significantly when marshes are flooded and points to several areas that need to be investigated further. What environmental factors in flooded marshes favor the growth of metaphyton? Changes in light conditions and nutrient concentrations with flooding particularly need to be investigated. Why is metaphyton biomass highest within stands of emergent litter in flooded marshes? Do these algae simply become trapped there, or are environmental conditions within this habitat more conducive to the growth of these algae? What is the relationship between the production of metaphyton, phytoplankton, and epiphyton in a marsh? What is the contribution of metaphyton to the overall annual production of marshes? What impact does metaphyton production have on invertebrate populations in flooded marshes?

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